THE ROLE OF WINTER TEMPERATURES IN DETER-MINING THE DISTRIBUTION OF PLANTS[1]

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The investigation of the control of plant distribution by the various phases of the temperature factor is one of the most important tasks of physiological plant geography, at the same time that it is one of the most backward and difficult. The field is an old one, the first outlines of which were sketched by Willdenow, Humboldt and Schouw. They delimited the great temperature zones of the earth, but in relation to flora rather than to vegetation,—in relation to the distribution of species, genera and families, rather than to the great physiologically coherent assemblages of plants. To the investigations and explorations of these men and their immediate successors we owe the dictum (which is itself of later origin) that the character of the flora of a region is controlled by temperature, that of its vegetation by moisture.

The only temperature datum used by the early plant geographers was the annual mean, and this is still used as the sole criterion in distributional studies by men who prefer that their generalizations should be broad rather than of scientific utility. The gigantic toil of the phenologists between 1850 and 1890 yielded some results on the operation of temperature, and gave us a vast accumulation of data of which some real use was made at the time, and to which we may return in future investigations. The men by whom this work was carried on were mostly climatologists, and their efforts were handicapped by the fact that they worked extensively rather than intensively, and that they had not a sufficient foundation of physiological facts upon which to operate.

Our knowledge of temperature influences in the distribution of vegetation is fundamentally underlaid by our knowledge of temperature influences on individual species of plants, and the two bodies of knowledge have come from fields of study which are widely unlike in their perspective and methods: from geography and from plant

physiology.   The viewpoint of the geographer—and with him that
of many floristic plant geographers—is too broad and general to give
due regard to the actual physiological effects of temperature on plants;
the point of view of the plant physiologist, on the other hand, is often
too intensive to enable him to realize that the "conditions" of his
laboratory experiment are identical with the "physical factors" of
the environment of plants growing under a state of nature, and he is
therefore prone to neglect the bearing of his work on the problems of
the field.   There is no greater desideratum at the present time—with
respect to the operation of all environmental factors—than to bring
the intensive methods and exactness of logic which characterise
physiological work to bear on the large and intricate problems of
physiological plant geography.

In a consideration of the influence of the various phases of the
temperature factor on the limitation of the distribution of plants, and
on their relative abundance in different parts of their areas, it will
be seen that these phases fall into two well-marked groups.   The
first to be mentioned—and neither can be first in importance—
are those phases of temperature which have to do with the length of
the season in which growth and other activities are possible, with the
curve of temperature conditions within this season, and with the
possible effect of the highest portions of the seasonal curve as deterrent
to the activities of plants.   The second group of phases of the tem-
perature factor are those which have to do with the length of the
season during which low temperatures may exert a deterrent or fatal
effect upon physiological activities, and with the duration and intensity
of the critical periods in this season.

Considerable physiological study has been given to the effect of
gradients of temperature upon plant activities, and also to the effect
of various durations and intensities of cold.   Various attempts have
been made to formulate the results of these physiological investigations
in such a way as to give them general applicability in plant geography,
and of these attempts it may be said in general that each has been an
improvement upon its predecessors.   It has been one of the most
common errors of the phenologists that they have considered a degree
at one part of the temperature scale the equivalent of a degree at
another part of the scale.   This impossible assumption has led to the
totalling of daily mean temperatures as the means of securing an index
of the possibilities for plant existence or plant growth in a given

locality.   Thanks to the growing interest manifested in this subject
by men with physiological training, the crudities of the earlier work
are being eliminated from the most recent utterances on this subject.

One of the most widely used schemes for the formulation of tem-
perature data in such manner as to give them general applicability
in biogeography, is the system of life zones proposed by Merriam for
North America.   These zones are based on the isothermal lines which
indicate the totalled degrees of temperature for the growing season.
Not only does the placing of such lines rest fundamentally upon the
assumption that every degree of temperature is the equivalent of
every other degree in respect of plant activity, but it takes no account
whatever of the second phase of temperature effects which are exerted
in the frost season.

Not only is Merriam's scheme of life zones to be criticized as a
geographical delineation of temperature conditions, but it is even
more fundamentally faulty when it is urged as a general scheme of
classification of biogeographical regions.   In spite of the importance
of temperature as a factor in distribution it is illogical to take it as the
sole criterion for the limits of distributional regions, especially when
the rôle of soil and atmospheric moisture is so obviously of vital im-
portance and is so potent in determining the areas of the principal
vegetational regions of the globe.

The temperature phases of the growing season and those of the
frost season are in no respect reciprocal or complementary to each
other, excepting in the mere matter of the length of the two seasons.
The end effects of the temperature conditions of summer and those of
winter are quite distinct as they are registered in the limitation of
the range of species.   In the case of plants which range over large
areas it is quite commonly the winter phases of temperature which
limit their northward distribution, and the summer phases which
restrict them at their southern edge.   In many other cases it is the
summer phases which determine the northern limit of the conditions
that make it possible for a species to grow.

More attention has been given by phenologists to the temperature
phases of the growing season, and their potentialities, than to those
of the frost season.   The writer has welcomed, therefore, an oppor-
tunity to make some preliminary investigations of the importance of
the temperature phases of the frost season in determining the distribu-
tional limits of some sub-tropical desert plants.

The Desert Laboratory is situated near the northern edge of a botanical province which extends far southward into Mexico, and includes in its flora many Mexican plants which do not penetrate more than a few hundred miles into the United States.   Within easy access of the Laboratory are three ranges of mountains which rise from the desert floor, at 3,000 ft., to elevations of over 9,000 ft.   The slopes of these ranges present rapid gradations of climate and successive changes in vegetation, from cacti and thorn-shrubs at the base, through junipers and evergreen oaks to extended forests of yellow pine, and above them to heavy stands of spruce and fir.   The lower limit of the juniper-oak chaparral is about 4,500 ft., that of the pine forest about 6,500 ft.   The rugged topography of the slopes gives alternations of exposure and local departures from the normal gradients of both climate and vegetation, which greatly heighten the interest and fruitfulness of the mountains for investigation.

The lower limit of the chaparral and forest plants, and their failure to reach the desert, is to be attributed to the ratio between the soil moisture and the evaporation in the early summer, which is a period of extreme aridity below an elevation of 5,000 ft.   It is not logical to dismiss the possibility that some phase of the summer temperature conditions may operate also to limit the distribution of mountain plants at the edge of the desert.   Even if this were found to be the case, the results would bear scrutiny in the light of recent work done at the Desert Laboratory which demonstrates a close relation between the temperature of the aerial organs of plants and the maintenance of their absorption-transpiration balance.

The upward limitation of the subtropical desert species is to be attributed to the winter phases of the temperature conditions, as has been determined both by experimental evidence and by correlation of the results of instrumentation with observations of the vertical limits of species.

An attempt to determine the normal temperature gradient in the Santa Catalina Mountains from 3,000 to 8,000 ft. disclosed the very great importance of inversions of temperature in causing local departures from the normal gradient.   The rapid nocturnal cooling of the desert soil—which is hastened by its dryness, its prevailing stony or sandy character, and its scant cover of vegetation—is responsible for a pronounced settling of cold air into the valleys and depressions, where it possesses a flow and a definite depth in close analogy to streams

of water. A comparison of the average monthly minimum temperatures which prevail at the Desert Laboratory and in the bottom of the Santa Cruz valley, has already been published by the writer.[2] The extensive drainage basin of the Santa Cruz, which is bordered by high ranges of mountains, receives the cold air flow of such a large area that the minimum temperatures in the floor of the valley are always much below those of the Desert Laboratory, situated 335 ft. above the valley, but only half a mile from its edge. The difference between the valley and laboratory minima is greatest on the clear, windless nights of spring and autumn, when the valley temperature has been as much as 31° F. (30° and 61°) below that of the laboratory. The difference between the monthly mean minima for May is 17.8°, that for June 14.4°, both of these months being dry and their nights prevailingly clear. On cloudy nights after heavy rains the minima of the two places have approached within 2° (69° and 71°), that of the valley being lower. The difference between the monthly mean minima for July and August are respectively 7.7° and 8.8°, these months being relatively cloudy and damp.

In Soldier Cañon, at an elevation of 5,000 ft. in the Santa Catalina Mountains, the temperature of the floor of the cañon has been observed to be 8° below that of the slope of the cañon 100 ft. above the floor. In Bear Cañon, at 6,000 ft. elevation in the same range, the minimum in the floor of the cañon has been observed 7° lower than the minimum of the rim of the cañon 1,000 ft. above. Observations 100 ft. above the floor would probably have revealed an even greater difference. The walls of both these cañons are clothed with open stands of desert and chaparral plants, the latter cañon having extremely rocky walls. In Marshall Gulch, at 7,725 ft. elevation in the Santa Catalina Mountains, the minimum temperatures are identical in the bottom of the gulch and on its rim 275 ft. above. The walls of this gulch, or cañon, are heavily covered with forests of pine, spruce and fir. The drainage areas of the three mountain cañons are, in each case, much smaller than that of the Santa Cruz river.

Our knowledge of the conditions which make cold air drainage possible in the desert, leads us to anticipate that it would be less well marked, or even absent, at the heavily forested altitudes of the desert mountain ranges. The diurnal heating of the soil and other surfaces is not so great in the forest, and the nocturnal radiation is retarded

[2] Shreve, Forrest. Cold Air Drainage. The Plant World **15**: 110–115, 1912.

not only by the forest cover but by the surface litter of the soil, and by the greater humus content and moisture content of the soil.

The marked character of the temperature inversions has made it necessary, in determining the temperature gradients of the Santa Catalina Mountains, to compare only the stations which are in topographically similar situations. It also makes it necessary to compare separately the gradients of the desert and those of the forested altitudes.

The absolute minimum temperatures of the winter of 1912–13 at several mountain stations showed that there was a successive fall of minimum from 17° at the Desert Laboratory (2,663 ft.) to 13° at 4,000
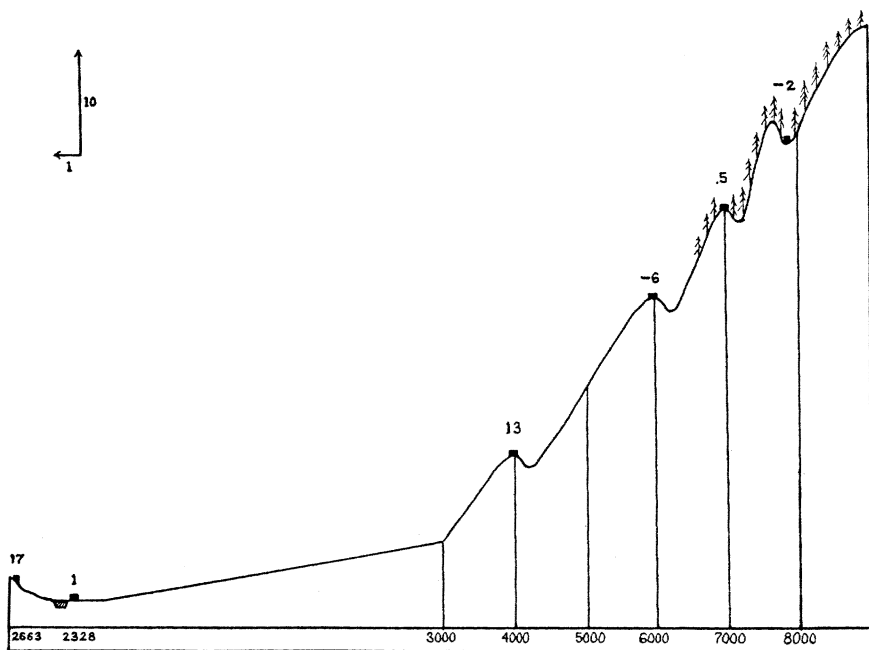

FIG. 1. A vertically exaggerated section from the Desert Laboratory to the summit of the Santa Catalina mountains, to show the elevation and topographic location of temperature stations, together with the absolute minima of the winter of 1912–13.

ft., and − 6° at 6,000 ft. There was then a rise of minimum to .5° at 7,000 ft., the first station in the forest, and a fall to − 2° at 7,725 ft. (see Fig. 1). Similar figures were secured in the winter of 1911–12,

showing the lowest absolute minimum for the mountain to occur not at the highest station, but at the highest station below the forested elevations. The absolute minimum in the heavy timber at Marshall Gulch was 4° higher than it was 1,700 ft. below in an open stand of manzanitas and oaks, a phenomenon in which cold air drainage was not concerned, since the higher station was in the timber and the lower on a ridge.

The strongly defined character of the cold air drainage of the Santa Cruz valley can be appreciated from the fact that the absolute minimum recorded in the valley was 1°, only three degrees higher than the absolute minimum 5,400 ft. above in the forested region of the Santa Catalina Mountains.

The mean gradient of fall in temperature with increase of altitude, averaged for a large number of mountains in different latitudes and climates, indicates a fall of 3.46° per 1,000 ft. This gradient happens to be identical with that for Pikes Peak. The steepest gradient previously recorded is 4.12° per 1,000 ft., for the western slope of the Sierra Nevada. The gradient for the Santa Catalina Mountains has been determined by comparing the daily mean temperatures of the Desert Laboratory with the daily means secured from observations at the Montane Plantation of the Laboratory and at Mt. Lemmon (alt. 9,150 ft.). This comparison evades the influence of cold air drainage by reason of the fact that both the laboratory and the forested altitudes are beyond its effects. The value of the gradient thus determined is 5.2°, or more than one degree higher than the highest gradient previously reported, and differing from the maximum reported gradient more than the said maximum differs from the mean of all reported gradients.

The gradient derived from the absolute winter minima of the Desert Laboratory and of the ridge stations at 4,000 and 6,000 ft. is 6.6° per 1,000 ft. The gradient above the commencement of timber is 2.5° per 1,000 ft. The gradient of temperature fall in the free air has been determined at the Blue Hill Observatory, for low altitudes, as 2.16° per 1,000 ft.

The streams of cold air which flow from the mountain cañons are shallow, never exceeding 75 ft. in depth, and often being less than 50 ft. Below elevations of 6,000 ft., by virtue of these streams, the minimum temperature conditions of cañons and other topographic depressions are equivalent to those of ridges and slopes which lie

about 2,000 ft. higher. The vertical limits of a large number of species have been found to differ by this amount as determined for cañons and for ridges and slopes.

It would appear, therefore, that the winter phases of the temperature factor sustain, in their distribution, a close relation to the distribution of plants. The experimental work carried out to test this correlation was planned only after a study of the relation existing between the vertical distribution of several plants throughout Arizona, and the vertical distribution of several phases of low temperature. Data were secured from a series of Weather Bureau stations extending from the low southwestern corner of Arizona to the cool highlands of the northern part of the state. The length of the frost season, the number of days with freezing temperature, the total number of hours (per winter) of below-freezing temperature, the greatest number of consecutive hours of frost, and the lowest minimum have all been ascertained, not in their average, but in their maximum intensity. The results indicated that the greatest number of consecutive hours of freezing temperature is the factor most closely corresponding, in its distribution, with the limitation of the species concerned.

Experiments performed[3] with succulent plants native to various altitudes in southern Arizona, indicated that the number of hours that they are exposed to temperatures below freezing determines their death, without regard to the absolute minimum reached during the freezing period (although minima below 18° F. were not used). The succulents which have the lowest vertical limit are unable to resist freezing over 19 to 22 hours in duration, while the species of higher and higher limits are progressively able to withstand longer and longer periods of freezing, up to 66 hours. With the limited hardiness of the Arizona species of cacti may be compared the behavior of *Opuntia missouriensis*, which withstood 375 consecutive hours of freezing temperature in the winter of 1910–11, at Havre, Montana, near the northernmost limit of the succulent type of plant.

There are doubtless species other than those investigated in which the absolute minimum attained during freezing is of critical importance in causing death; there are doubtless very low minima (never attained in Arizona) which would be fatal on very short exposure; and there are probably still other species of plants for which some of the other

[3] Shreve, Forrest. The Influence of Low Temperatures on the Distribution of the Giant Cactus. The Plant World 14: 136–146, 1911.

winter temperature phases mentioned are of paramount importance as limiting factors.

It is impossible to speak authoritatively of the importance of the temperature conditions of the growing season or those of the frost season in their relation to vegetation as a whole until we posess a large body of data regarding their influence on individual species. It is fundamentally important, furthermore, that our knowledge of the influence of these and other physical factors should be secured by observation of the distributional limits and behavior of species, by instrumentation, calculated to single out the critical factors and their critical intensities, and finally by investigation, in the laboratory, of the operation of these factors and of these intensities.   Only in some such manner as this is it possible actually to interpret the underlying causes of the phenomena of distribution.   Thus only can the observed or the instrumentally determined correlations of the field be given confirmation.   Thus only can physiological plant geography place its generalizations on a secure logical basis.

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